A NEW SPECIES OF THE LYCOPSID *PLEUROMEIA* FROM THE EARLY TRIASSIC OF SHANXI, CHINA, AND ITS ECOLOGY

by WANG ZIQIANG *and* WANG LIXIN

ABSTRACT. A new species, *Pleuromeia jiaochengensis*, is recorded from the early Triassic of Jiaocheng district in Shanxi (Shansi) Province, China. Its small size, morphological features of the strobilus and sporophylls, abortive leaves, and the undeveloping rhizophore separate this from all other species. The succulent sporophylls may be a major area of photosynthesis. Based on lithology and distance from known marine strata, an inland desert environment is suggested for this new species. Its stratigraphic significance is discussed.

IT is well known that Palaeozoic floras flourished during Upper Carboniferous and Permian time, but suffered from a worldwide arid climate at the end of the Permian. Only a few relics survived into the early Triassic where they faced severe climatic conditions. One such genus is *Pleuromeia* which is regarded as an important early Triassic index fossil, and thought to be a link between the Palaeozoic *Sigillaria* and modern *Isoetes*.

Pleuromeia was first recorded from the Bunter Sandstone in Germany nearly a century ago. Prior to 1960, apart from a few records from France, Spain, and the eastern U.S.S.R. all the records were from Germany. In particular, Mägdefrau (1930, 1931) provided much information about the genus from a large number of German specimens.

Since the 1960s new material has been recorded from the early Triassic in the Soviet Union, Japan, and China. *Pleuromeia rossica* was described by Neuberg (1960*a*) from the Russian Platform, whilst Krassilov and Zakharov (1975) added further information on the genus from material in the far eastern part of the Soviet Union. Kon'no (1973) described *P. hatai* from the Scythian in north-eastern Japan, and in China, Wang, Xie, and Wang (1978) described well-preserved specimens of *P. sternbergi* (Münster) Corda and *P. rossica* Neuberg from the early Triassic of the Qinshui Basin in Shanxi. The genus *Pleuromeia* therefore has a widespread distribution. It is worth noting that from the early Triassic of eastern Australia, *Cylostrobus* a lycopsid-like strobilus which shows some similarity to *Pleuromeia* of the Northern Hemisphere, has recently been regarded by Retallack (1975) as *Pleuromeia longicaulis* (Burgess).

After the discovery of *P. sternbergi* and *P. rossica* from the early Triassic Heshankou Formation in Qinshui Basin, Shanxi Province, the present writers found many well-preserved specimens belonging to a new species of *Pleuromeia* in the Luijiakou Formation beneath the Heshankou Formation in Jiaocheng district (text-fig. 1), not far from the famous Xuan-zhong Temple of Shanxi Province. This paper describes these specimens.

FOSSIL-BEARING STRATA

The Luijiakou Formation in Jiaocheng district is the western extension of the sandstone beds of the 'Shischienfeng Series' at West Hill in Taiyuan, and consists mainly of reddish-purple, fine-grained sandstones. According to data supplied by the Regional Geological Survey of Shanxi Province, its thickness in Jiaocheng district exceeds 460 m, the Formation being subdivided into three parts. The upper part, consists of 108 m of grey and reddish-purple fine-grained feldspathic sandstones intercalated with reddish-purple siltstones and sandy shales. The middle part is composed of 215 m of red, grey to greyish-purple fine-grained feldspathic sandstones interbedded with reddish-purple silty shales and shales. The shales contain abundant ripple marks,

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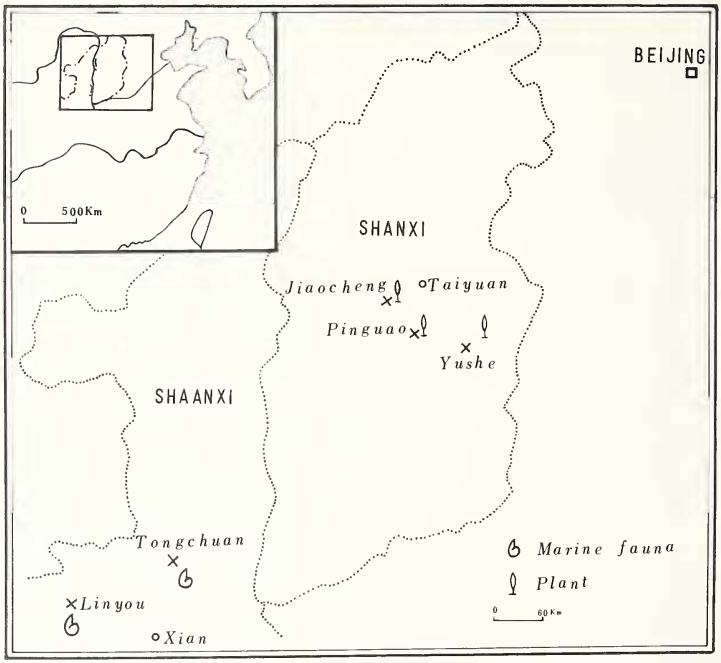
sun-cracks, and cross-bedded structures sometimes intercalated with a few lenses of greyish-white sandstones containing fossil plants and greyish-green shales with fossil estherians. The lower part, consists of 138 m of reddish-grey and purplish-grey fine-grained, cross-bedded feldspathic sandstones containing abundant laminations of magnetite, intercalated with lenses of greyish-white feldspathic sandstones. The fossil plants, which include *Pleuromeia*, are within the middle part of the Formation approximately 130 m above its base at four localities (numbered Z01–Z04) near Jaoertou village, in the north-western mountainous area of



TEXT-FIG. 1. Map showing region of the fossiliferous localities. Inset shows eastern half of China.

EXPLANATION OF PLATE 23

All figures ×1 unless otherwise stated. All specimens from the Luijiakou Formation, Shanxi Province.

Figs. 1–13. *Pleuromeia jiaochengensis* sp. nov. 1–2; 6–11. Various strobili; 1, Z01–021; 2, showing the awl-like leaves on the part of stem beneath the strobilus, Z01–01; 6, Z01–024; 7, Z01–027; 8, Z01–019; 9, Z01–022; 10, Z01–019; 11, syntype, a strobilus containing megaspores (at a), Z01–061. 3–5, complete young plants; 3, syntype, Z01–020; 4, the same ×4, 5, Z01–061. 12. Shows a decorated stem, with short surface ridges, Z01–061. 13. Syntype, stem surface showing sparse, faint leaf-scars, Z01–206, ×2.

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Jiaocheng district. At locality Z01, there are many well-preserved specimens of strobili, stems, rhizophores, and even some complete plants in a lens of greyish-white sandstone, 0·2 m thick and 2 m across. At Z04, there are many sporophylls, stems, and rhizophores occurring in larger lenses. In addition, at localities Z02 and Z03, there are specimens tentatively included within the genera *Crematopteris* sp. *Phyllotheca* sp. *Taeniopteris* sp. *Neocalamites* sp. by the present authors. All specimens illustrated in this paper, are reposited in the Tianjin Institute of Geology and Mineral Resources, Ministry of Geology.

SYSTEMATIC PALAEOBOTANY

Family PLEUROMEIACEAE
Genus PLEUROMEIA Corda, 1852
Pleuromeia jiaochengensis sp. nov.

Plates 23, 24, text-figs. 2–3

Syntypes. Z01–020 (small complete plant); Z01–061 (showing strobilus and megaspores; Z01–206 (showing stem surface); Z04–159 (showing rhizophore).

Diagnosis. A lycopsid of small shrub size, probably dioecious, generally 20–30 cm high but may reach almost 50 cm (see text-fig. 2, the reconstruction of a whole plant). Stem erect, unbranched, maximum diameter 1·5 cm, terminating in a large strobilus measuring one-quarter to one-third of the plant height (Pl. 23, figs. 3–4). Surface of stem covered with sparse, faint, at times barely visible leaf-scars, usually smooth, with small obscure pits where the leaves were originally attached. Decorticated stems with short ridges (Pl. 23, fig. 12). Leaf-scar lens-shaped, obscure in outline, with a central pit (Pl. 23, fig. 13). Leaves awl or spine-like, 2–3 mm in length, about 1 cm apart on the upper portion of the stem (Pl. 24, fig. 6), having dehisced from the lower part. Rhizophores tuberous when mature, covered with oblong to oval, well-separated appendage-scars; the younger rhizophores only slightly swollen at the base of the stem and covered with rather thick appendages, maximum length 3 cm, usually on the lower part. Strobilus probably unisexual, narrowly spike-shaped, maximum length 20 cm. Sporophylls spirally arranged, imbricate, 4–5 in each spiral (Pl. 23, fig. 6), the spiral from 60° to quite an acute angle to the rachilla, giving a total of more than 100 sporophylls in a mature strobilus. Sporophylls spatulate with a sagittate apex, longer than wide, ovate to oblong in outline, adaxially concave where the sporangium lies. The border of the sporophyll is wider anteriorly than laterally, and in mature strobili the apex of the anterior border of larger sporophylls is slightly reflexed upwards (Pl. 24, fig. 3; text-fig. 3*d* left), and is probably visible on the outside of the strobilus. Where the upward reflexed part of a sporophyll is truncated, it clearly shows a retuse, small anterior border (Pl. 24, fig. 5). Sporangium discoid, oval or orbicular in outline, attached to the rachilla only at its proximal end. Surface of sporangium with many more or less parallel lines (Pl. 24, fig. 4) which converge slightly at both ends. Thickness of

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EXPLANATION OF PLATE 24

All figures ×1 unless otherwise stated. All specimens from the Luijiakou Formation, Shanxi Province.

Figs. 1–15. *Pleuromeia jiaochengensis* sp. nov. 1–2. Part of strobili containing megaspores (at *a*). 1, Z01–01, ×2. 2, an enlargement of syntype, Pl. 21, fig. 11, showing megaspores associated with nearly all the sporophylls. 3–5. Sporophylls and sporangia. 3, two sporophylls, the right one with upward reflexed apex, Z01–08 ×2; 4, sporangia near base of a strobilus, showing the parallel lines on their surface, Z01–042; 5, a larger sporophyll having lost its reflexed apex, Z01–061. 6. Part of a stem, showing spine-like leaves, Z01–00. 7. Enlargement of a sporangium containing megaspores (*a*), from the strobilus of Pl. 21, fig. 11, Z01–019, ×10. 8. A megaspore, Z01–022, ×50. 9–15. Various rhizophores; 9, 10, showing appendage scars, Z01–060, Z01–135; 11, on the right, a young rhizophore showing a few appendages on the lower part, Z01–054; 12, the same ×2; 13–15, showing appendages on the lower part, and appendage scars on the upper part; 13, Z01–027; 14, Z04–151; 15, syntype, Z04–159.

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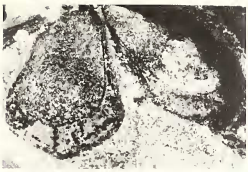
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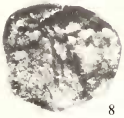
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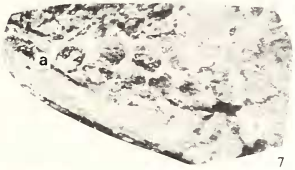

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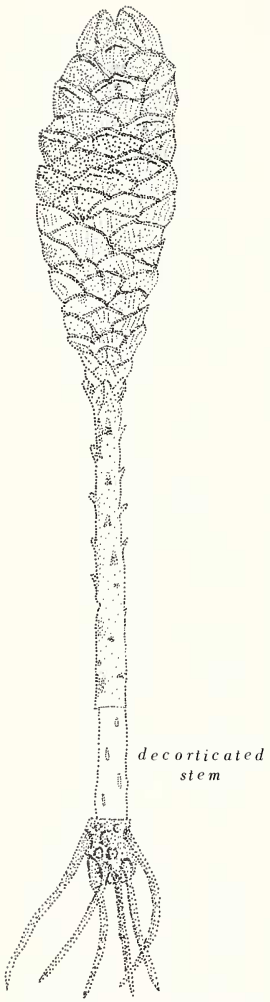


TEXT-FIG. 2. *Pleuromeia jiaochengensis* sp. nov. Reconstruction of a whole plant, × 1.

sporangium decreases gradually from proximal to distal end, resulting in an aggregation of spores at the proximal end near the rachilla. Megaspores tetrad, spherical or triangular, laevigate or granulate, 300–500 μm in diameter. Trilete mark distinct, shorter than spore radius. Microspores unknown.

Discussion and comparison. The single, erect, terminal strobilus terminating on unbranched woody stem, are characters associated with the genus *Pleuromeia* rather than *Selaginella* or *Isoetes*. Though the sporophylls of this new species have an elongate anterior border similar to those in *Selaginella*, they differ from it in lacking elongate acuminate distal tips (Retallack 1975). Also, the thick, spatulate shape is quite unlike the sporophyll of *Selaginella*. In addition, *Selaginella* is herbaceous with a dichotomous stem and dimorphic leaves often in four rows (Chaloner 1967; Smith 1955), quite unlike those of *P. jiaochengensis*.

Isoetes, which is usually considered a close relative of *Pleuromeia*, lacks a definite stem from the lobed rhizophore, and also lacks a distinct strobilus. Unlike *Pleuromeia*, the sporophylls of *Isoetes* are placed within the centre of a cluster of leaves.

In the past, when identifying species of *Pleuromeia*, authors have placed considerable emphasis on features of the leaf-scars on the stem surface. During the past two decades, more recent finds have greatly increased knowledge of the reproductive organs; for example, the strobilus, sporophylls, sporangia, megaspores, and microspores. These are now used much more in identification. Also, Dobruskina (1974) pointed out that the leaf-scars on specimens assigned to *Pleuromeia* and *Pleuromopsis* by Brick (1936) and Sixtel (1962) respectively, from the late Triassic of Central Asia, are not from these genera, and that the leaf-scars of *Pleuromeia* vary in shape depending on the degree of decortication prior to burial. Some specimens from the late Permian of the Petchora Basin in the Soviet Union included by Neuberg (1960*b*, pl. 5, fig. 2; pl. 14, right) in the genus *Viatscheslavia* have similar leaf-scars to those in *Pleuromeia*. Hence leaf-scar features are not now considered as important as in the past in identifying *Pleuromeia*.

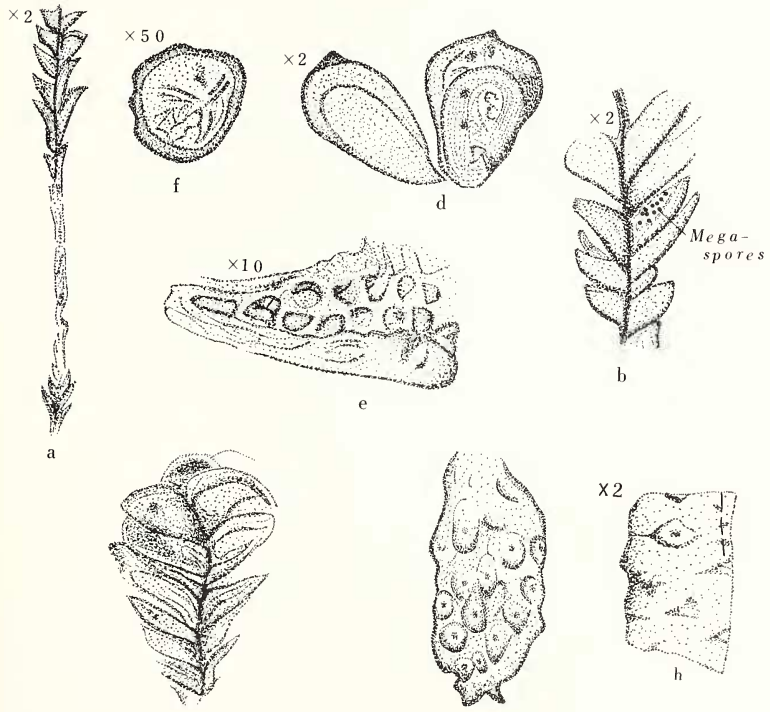
Of the six previously described species of *Pleuromeia* from the Northern Hemisphere, only three, namely *P. sternbergi*, *P. rossica*, and *P. hatai*, have been found in sufficient numbers and are well preserved enough to give knowledge of the complete plant. Of the rest, there is not enough real evidence for their assignation as distinct species. *P. oculina* (Blanckenhorn, 1886) lacks reproductive organs, *P. olenekensis* (Krassilov and Zakhalov, 1975) is too incomplete to compare with other species, and the designation of *P. obrutschewi* Elias is in dispute (Krassilov and Zakhalov 1975).

P. jiaochengensis differs from all previously described species, by its small size, relatively large strobilus with elongate

sporophylls, and its undeveloping rhizophore with appendage-scars which are less in number, and larger. *P. jiaochengensis* is usually 20–30 cm high, with a maximum height of under 50 cm. This compares with 2 m in *P. sternbergi* and 1 m in *P. rossica*. The smallest specimens of *P. hatai* may be of similar size.

The strobilus of *P. jiaochengensis* is larger in proportion to the whole plant than in other species, except *P. hatai*. The strobilus of *P. hatai*, however, differs from *P. jiaochengensis* in being cylindrical rather than spike-shaped. Also, in *P. hatai* there are more sporophylls in a strobilus, and they are smaller in size.

The sagittate shape of the sporophyll of *P. jaiochengensis* is slightly different from that in all



TEXT-FIG. 3. *Pleuromeia jiaochengensis* sp. nov. *a*, complete young plant, ×2; *b*, a strobilus with megaspores, ×2; *c*, a strobilus, ×1; *d*, two sporophylls, the left one with an upward reflexed apex, ×2; *e*, a sporangium containing megaspores, ×10; *f*, a megaspore, ×50; *g*, a rhizophore covered with appendage-scars, ×1; *h*, a stem surface with a few leaf-scars, ×2.

other species. Plate 24, fig. 5, right, shows a larger sporophyll of *P. jiaochengensis*; its upward reflexed tip having been truncated, exposing a retuse anterior margin which differs from *P. rossica*, in having a notched margin (Pl. 24, fig. 5). In *P. sternbergi* the mature sporophylls also have an elongate outline, but unlike *P. jaiochengensis* the lateral and anterior margins are of approximately equal width.

Although the nature of the sporangium of *P. jaiochengensis* is not as yet clear, the uniform megaspores are different from those in *P. rossica*, but similar to those in *P. sternbergi* and *P. hatai*. However, unlike these two species, the sporangium has a markedly thickened proximal end (Pl. 24, fig. 7; text-fig. 3*e*), which contains a mass of megaspores.

The awl or spine-like leaves of *P. jaiochengensis* is one of the most important characters in comparing this with other species. No clear leaf-scars are present after the leaves have dehisced. The leaves of *P. sternbergi* and *P. hatai* are linear in outline and, after dehiscence, leave obvious leaf-scars on the outer stem surface. The leaves of *P. rossica* are probably scale-like (Dobruskina 1974), and rather similar to those in *P. jaiochengensis*, but when dehisced they leave densely covered and distinctive leaf-scars.

An undeveloping rhizophore is also regarded by the present writers as an important character for distinguishing the new species. Its appendage scars are larger and less in number than other species. In addition, unlike the other species, the rhizophore has neither horns nor suture lines (klüfte) on the lower surface.

When describing *Pleuromeia* from the Qinshui basin of Shanxi, Wang *et al.* (1978) noted that the difference between the strobili of *P. sternbergi* and *P. rossica* was so great that, as pointed out by Kon'no (1974), they might represent different genera. With regard to this, *P. jaiochengensis* throws more light on *P. sternbergi* based on its unisexual strobilus without a pedicel, and on the character of the sporophylls.

Retallack (1975) transferred the lycopsid-like strobilus *Cylostrobus* (originally designated by Helby and Martin 1965) which had previously been considered more like the palaeozoic lycopsids, to *Pleuromeia longicaulis* (Burgess). The specimens are from the early Triassic of eastern Australia, and is the first record of this genus in the Southern Hemisphere. This type of strobilus shows some important features, for example, it is bisexual (monoecious), the sporophylls have a remarkable ribbed keel-like apex on their dorsal surface, and the microspores are monolete and covered with dense spines. All these features are strikingly different from Northern Hemisphere *Pleuromeia* species, including *P. jaiochengensis*. The basis for the designation of the Australian species given by Retallack, mainly results from an analysis of their environment and a few associated fossil stems. In fact, there are two types of stems associated with *Cylostrobus sydneyensis* from the upper Narrabeen Group; one bearing a stigmaria-like stem-base, and the other with branchlets (Helby and Martin 1965, p. 399, pl. 1, fig. 6) more like a palaeozoic lycopsid than *Pleuromeia*. The present authors are not as yet convinced that this Australian species should be included within the genus *Pleuromeia*. Recently, Ash (1979) has described *Skilliostrobus*, a new type of lycopsid strobilus also from the early Triassic of Australia, and this is similar to *Cylostrobus* in having bisexual, monoecious features.

ECOLOGICAL PROBLEMS CONCERNING *P. JAIOCHENGENSIS*

Pleuromeia was originally regarded as a desert xerophyte similar to the present-day Cactaceae. More recently, linking the plant-bearing beds with associated sediments containing dolomite and halite, together with marine fossil animals, a marginal marine habitat was suggested. Mägdefrau (1931) was first to suggest an halophytic habitat for *Pleuromeia*. Hirmer (1933), Neuberg (1960*b*), and Kon'no (1973) have supported this view, and more recently Krassilov and Zakharov (1975) and Retallack (1975) have suggested a mangrove-type environment along the sea-shore, or marginally on deltas. This type of habitat is not envisaged for *P. jiaochengensis*. Unlike the records from western Europe, Siberia, and Japan, no marine animal fossils have been recorded from the strata containing *P. jiaochengensis* in Jiaocheng district. Also, there is no evidence for lagoonal sediments, with the absence of dolomite and halite, and only a few doubtful reports of gypsum.

According to the geological exploratory reports of the Shanxi Regional Geological Survey Team the Formation in this area contains a lot of unweathered minerals such as feldspar and magnetite. Cross-bedding, ripple marks, and sun-cracks are relatively common, and indicate an arid climate. The 'Shischienfeng Series' with marine intercalated beds are known only from Linyuao, and Tongchuan districts of north Shanxi (Shengsi), and are at least 300 km from the Jiaocheng district (see text-fig. 1 and Yin and Lin 1979). We therefore consider *P. jiaochengsis* to be a small plant growing near desert oases. As all specimens are found in greyish-green sandstones, the new species might grow very near or even partly in the water bodies. Its small size also suggests arid conditions; the undeveloped and abortive leaves probably resulted from extreme transpiration in an arid climate. The appendages are stout and strong, probably to withstand desert conditions. Further evidence for an arid environment comes from the Estheridae which are recorded from the shales intercalated with the plant-bearing sandstones. This type of small fauna is often found in temporary inland bodies of water.

Plate 23, figs. 3–4, show a small but complete plant which is only 3 cm high. The stem is almost smooth, the large strobilus is well developed at the apex, and has a few distinctive appendages at its base. The appendages are plano-concave and fleshy, and were probably succulent. They are more developed than the sterile leaves, and may well have carried out much of the photosynthesis.

TABLE 1. The stratigraphic sequence of the 'Shischienfeng Series' in Shanxi.

Early Triassic	Olenekian	'Shischienfeng Series'	Heshankou Formation	*Pleuromeia sternbergi* *P. rossica*
	Induan		Luijiakou Formation	*P. jiaochengensis*
Later Permian	Tartarian		Sunjiakou Formation	*Shihtienfenia permica*

STRATIGRAPHIC OCCURRENCE OF THE GENUS *PLEUROMEIA*, AND THE AGE OF *P. JIAOCHENGENSIS*

In Germany the *Pleuromeia*-bearing beds have a rather short vertical range, extending from Middle to Upper Bunter (i.e. from Bausandstein to Chirotheriumsandstein). The age according to Lozovsky, Movschovich, and Mimich (1973) is considered to be equivalent to the *Tirolites–Columbites* ammonite zone of Middle and Upper Olenekian age, despite the lack of the ammonite evidence. At Russian Island near Vladivostock and north-east Japan, *Pleuromeia* occurs in rocks of early Triassic age dated on the ammonites. On the Russian Platform, *P. rossica* occurs in the Ribinsk Formation together with the amphibian *Benthosuchus*, and is dated as early Triassic. According to Lozovsky *et al.* (1973), this Formation is equivalent to the *Owenites* ammonite zone, and may be referred to the early Olenekian.

At Mangeschlack near the Caspian sea, *P. sternbergi* occurs with marine lamellibranchs which also occur in the Upper Bunter Sandstone in Germany (Dobruskina 1974) and so are dated as late Olenekian. The *Pleuromeia* localities in the Vosges, at Mangeschlack in Central Asia, and on Russian Island in the Far East, are suggested by some authors as being as late as Middle Triassic. However, in the present writers' opinion, the exact age is in doubt, through lack of detailed information.

The Luijiakou Formation in central Shanxi is thought to be equivalent to the middle part of the so-called 'Shischienfeng Series'. For many years, no fossils were found, and the age was in doubt, but thought to be late Permian to early Triassic, depending on the exact age of the ?late Permian reptile *Shihtienfenia permica* Young, found in the underlying Sunjiakou Formation (see Table 1).

Recently Wang, Xie, and Wang (1978) described *P. sternbergi* and *P. rossica* from the overlying Heshankou Formation and suggested an early-middle Olenekian age for that Formation. The discovery of *P. jiaochengensis* in the Luijiakou Formation lends further support to the above age determination. In addition, another of the fossil plants associated with *P. jiaochengensis*, is *Crematopteris* sp. This species is confined to the Bunter Sandstone in western Europe. If the age of the Heshankou Formation containing *P. rossica* is referred to the Olenekian stage, or is equivalent to the Ribinsk Formation on the Russian Platform, then the age of the Luijiakou Formation can accurately be assigned to the Induan of early Triassic age.

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